

ONTOGENETIC CHANGE IN COLORATION AND WEB-BUILDING BEHAVIOR IN THE TROPICAL SPIDER *ERIOPHORA FULIGINEA* (ARANEAE, ARANEIDAE)

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ABSTRACT. *Eriophora fuliginea* (Araneae, Araneidae), a tropical orb-weaving spider from Panama, undergoes a dramatic color change in the course of its ontogenesis. The first free instar has an amber opisthosoma, which soon becomes bright yellow, later green. Subadults change to olive, adults are dark brown with a white median stripe. Parallel to this color modification the spider's behavior changes as well. The main activity phase shifts from day to night and web architecture changes from symmetrical horizontal orb-webs on the upper side of leaves with the spider on the hub, to asymmetrical horizontal orb-webs between shrubs with spiders in a rolled leaf nearby.

Keywords: Ontogenetic change, development, coloration, behavior, orb web

Quite often in the field, particularly in the tropics, one encounters colorful, juvenile spiders. When kept in the laboratory in many cases they change their coloration, frequently in a species-specific ontogenetic sequence. Since juvenile spiders normally cannot be identified, such coloration changes usually are not well documented, but may be very common. Only a few cases have been reported in the literature. The European sparassid spider *Micrommata virescens* (Clerck 1757) is an example of a spider of temperate regions where the males change from light green, to yellow, to greenish-yellow with red stripes or dots (Homann 1946). Bonnet (1929, 1930) describes the distinctive changes in color and pattern in *Nephila madagascariensis* (Vinson 1868). Edmunds & Edmunds (1986) report on two araneid species that show a distinct ontogenetic color change. *Araneus rufipalpis* (Lucas 1858) changes its color from a juvenile bright green, to a greyish-green or greyish-brown, to an adult dark brown. In *Gasteracantha curvispina* (Guérin 1837), the juvenile spiders are flecked white and brown, whereas the adults are white, yellow, orange, brown, red, or even striped in light and dark colors.

Different coloration of juveniles and adults within one species could indicate that different instars use different niches to reduce intraspecific competition. Such avoidance of competition between adults and their own off-

spring would be reasonable (e.g., Begon et al. 1996) and could include selection of different habitats, diurnal activities or food. An ontogenetic color change would support such important changes in a spider's life, but reports on the coincidence of color change and niche use are rare.

During an investigation on the prey composition of large orb-weaving spiders (Nentwig 1985), unknown small green juvenile spiders encountered during field research in Panama developed in the laboratory into dark brown adult spiders and were later identified as *Eriophora fuliginea* (C.L. Koch 1839) (Araneae, Araneidae). Later, dark brown females of the same species were caught in the field and built a cocoon in the laboratory from which amber juvenile spiders emerged. A sequence of the differently colored developmental stages was described in clutches of two females and was correlated to changes in the behavior that the juvenile spiders underwent as they matured.

METHODS

Two adult female *E. fuliginea* were caught in Panama (Parque Nacional Soberania, Gamboa) and brought to our laboratory. They were kept in cages (32 × 35 × 10 cm) made of wood and wire in a climate chamber (25–30 °C, 40–50% RH, L:D = 16:8 h), where they built one cocoon each on days 6 and 9 after

capture. After 29–32 days, the juvenile spiders hatched from the cocoons. The spiderlings ($n = 200$) were kept individually in transparent plastic boxes with lids ($20 \times 20 \times 8.5$ cm) which were set up on edge within a climate chamber (25–30 °C, 40–50% RH, L: D = 12.5:11.5 h). The bottom of each box was covered with plaster, which was kept damp to ensure a humidity within the boxes of approximately 100%. A cotton thread was attached to the inside of each box to provide fixing points for webbuilding. Flies of various species (*Drosophila melanogaster*, *Musca domestica*, *Calliphora erythrocephala*, *Protophormia terraenovae*) were provided *ad libitum* as food, with the fly size dependent on spider size. Due to high mortality especially in instars III and IV (days 20–40) and due to killing spiders for section preparations, only 40 spiders became adult.

The coloration and pattern of the growing spiders were recorded, sketched and photographed from hatching until their death as adult animals. The bases for the colorations and patterns were observed on live animals, on preparations of animals freshly killed with CO₂, and on sections. For each main color form, the opisthosoma of 2–3 freshly killed spiders were fixed in parts in 2% osmium tetroxide in potassium dichromate buffer according to Dalton (Glauert 1974). The preparations were then studied with the optical or electron microscope for the position of pigment granula. A white coloration is caused by guanine crystals which are deposited in guanocytes and can easily be recognized by the aid of Holl (1987). Yellow, red and brown colors are caused by different ommochromes, which are stored intracellularly as membrane-shielded granules. Green colors usually derive from linear tetrapyrroles (Holl 1987). No attempt was made to further identify the chemical basis of the colors.

Apart from recording the web building behavior with a video camera (one frame per second; night recordings with a lens sensitive to red light), the spiders were observed individually during the day, and at three different development stages during the night (22 animals on day 52 after hatching, 18 animals on day 90 and 16 adult animals on day 125). The observed activities were logged according to type and duration. The orb-webs were analyzed for differences between juvenile and

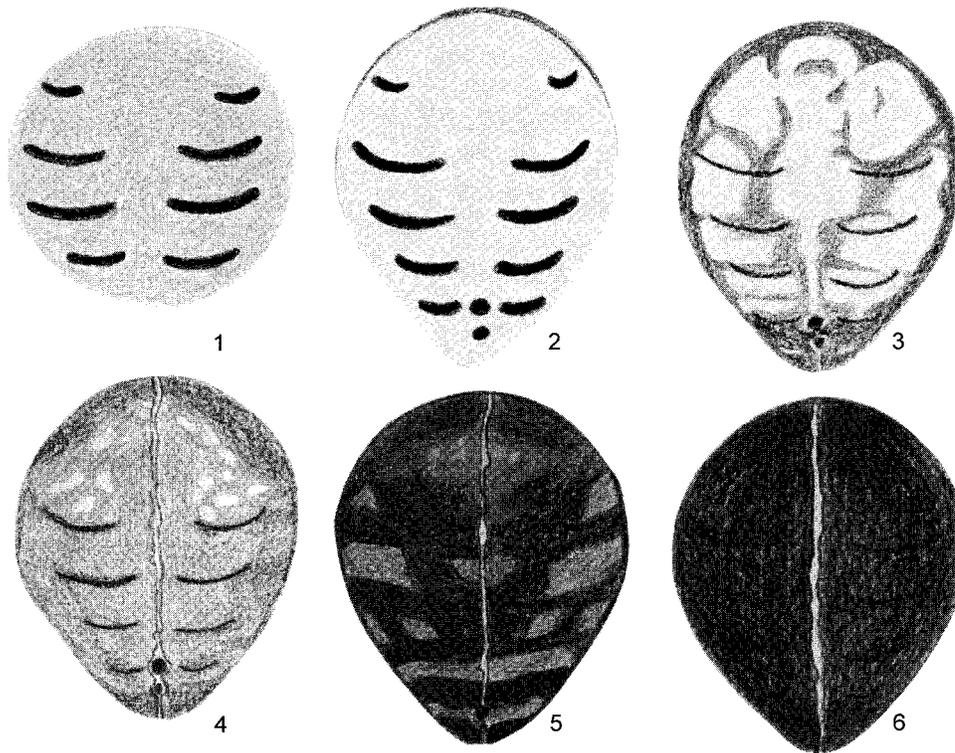
adult pattern, especially orb web symmetry and position of the spider in hub or retreat. Voucher specimens are deposited in the Natural History Museum, Basle, Switzerland.

RESULTS

Coloration and pattern.—The opisthosoma of freshly emerged juvenile spiders is amber, with three large and one small pair of black, slightly curved abdominal stripes on the dorsal side (Fig. 1). The diffuse deposition of guanine in the dorsal integument that begins frontally at approximately day 10 after hatching continues until the guanine is condensed to a tight layer between days 20–40 and causes a general lightening of the color. Parallel to this the opisthosoma turns from amber to bright yellow between days 15–60. The pattern expands with a fifth pair of abdominal stripes appearing with the second molting, two to three black median dots (small elevations in the cuticle filled with black pigments) and a posterior line. Simultaneously with the deposition of guanine, dark brown pigments begin to accumulate frontally on the opisthosoma, solidifying in the course of the next color change into a black band encircling the opisthosoma latero-dorsally (Fig. 2).

In most cases a shift from yellow towards green occurs at this time, which can be more-or-less pronounced: a) the color change either begins between the rear abdominal stripes and expands forwards, leaving the entire width of the frontal opisthosoma yellow and giving the entire opisthosoma a greenish-yellow cast, or b) the whole dorsal opisthosoma changes color, giving it a more yellowish-green cast before darkening to green (Fig. 7). The first variation can be found between days 17–67, the second between days 36–59.

The next color change initiates a darkening of the coloration. A longitudinally oriented V appears, which is first light brown in color, but darkens increasingly. As a result the dorsum becomes divided into a rostral and a caudal area. Based on the preceding color variation, different patterns ensue (Fig. 3): a) a tri-colored variation with a yellow area in front of, and a green area behind, the brown V, or b) a bi-colored variation with the brown V in the middle of the uniformly green opisthosoma. Male *E. fuliginea* show these variations between days 50–63, females between days 50–80 (Fig. 7).



Figures 1–6.—Color pattern of the dorsal opisthosoma of *Eriophora fuliginea*. 1. Instar I II; 2. Instar II-V; 3. Instar V-VII; 4. Instar VII (male), instar VII-VIII (female); 5. male, instar VIII-IX (adult); 6. Female, instar VIII-X (adult). Since color changes continuously irrespective of molting, the indication of instars is only approximative. *Scale*: Opisthosoma length of instar I is about 1 mm, adult females 15–25 mm. The colored version of these figures can be found at <http://www.cx.unibe.ch/zos/syn.htm> (go to publications, 2001).

As the V gets darker the abdominal stripes lose definition and blend into the pattern, changing color from black to a dark reddish-brown. Between the two legs of the V an off-white median stripe begins to form. In all color variations the areas in front of and behind the V change color in such a way that they appear olive-colored with either a yellowish, greenish or brownish cast. The anterior area tends to show a pattern of yellow and brownish-olive flecks, while the posterior area begins to display stripes of olive and brown. These variations appear in females between days 69–99 and in males between days 60–80 (Figs. 4, 7).

Between days 80–120 (females) and days 72–195 (males) the color shifts toward brown. In the males, the dark pattern of the dark brown V expands after approximately day 101, particularly towards the front, decreasing

the lighter area (lighter spots on medium dark brown). The contrast in the stripes becomes more pronounced with light (light brown or light greyish-brown) and dark (dark brown or brownish-black) stripes alternating. Additionally, short light hairs grow on the lighter stripes and short dark hairs grow on the darker stripes (Fig. 5).

In females, the V expands forwards as well, but less distinctly than in the males because of its lighter color. The anterior area stays lighter longer, sometimes flecked or mottled yellow or whitish on brown. The stripes in the posterior part shift towards brown and become less distinct. Most females develop a uniform dark brown to brownish-black coloration after this until the opisthosoma is only marked with a whitish median stripe (Fig. 6).

In both females and males the abdominal stripes turn a more reddish-brown during the

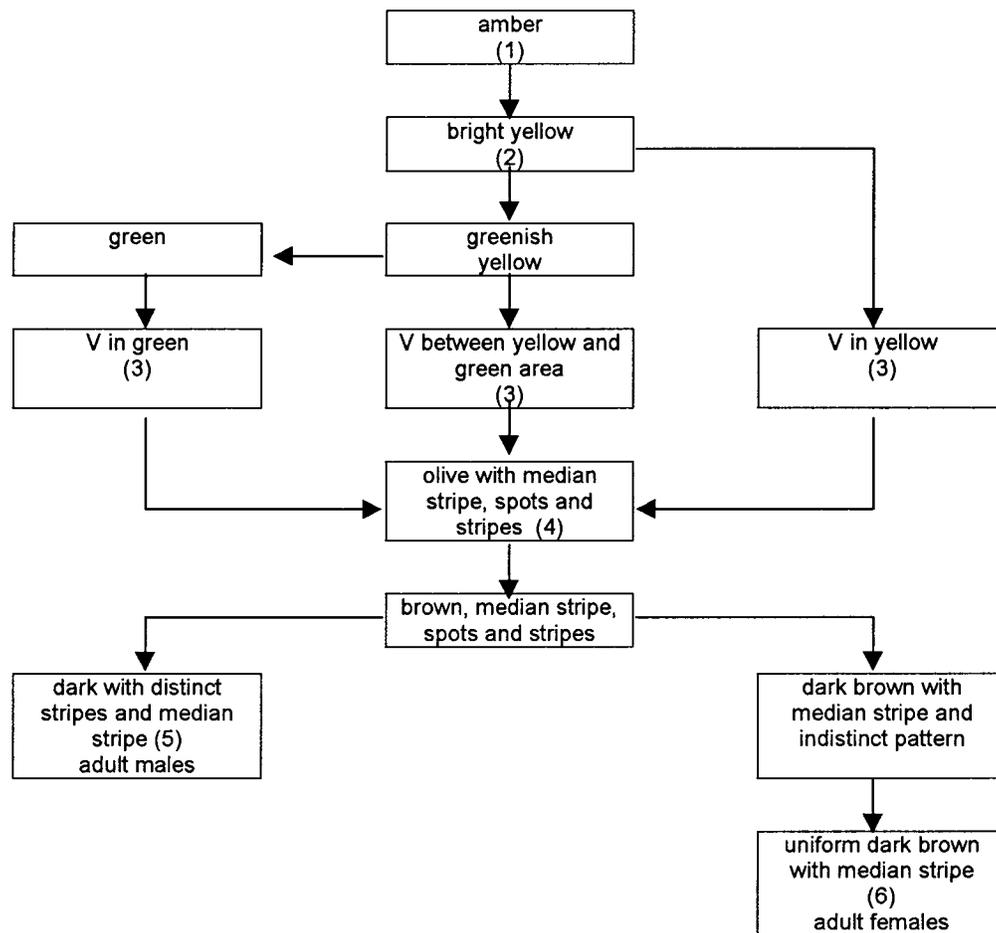


Figure 7.—Sequence of color changes in the dorsal opisthosoma of *Eriophora fuliginea*. Numbers refer to Figs. 1–6.

last two or three color changes, becoming thinner and less distinct, until they are only recognizable as hairless borders in adult females. The caudal median black spots are found in all animals except in adult females where they dissolve. In addition to these patterns many animals show variations in color, spots and stripes which we consider to be individual modifications.

Color origin.—The various colors of *E. fuliginea* have different origins. The amber color, particularly of the juvenile spiders, is based on the transparent coloration of the cuticle. With increasing thickness of the cuticle the amber becomes darker (dark amber to reddish-brown), e.g., in the prosoma of older animals, where the cuticle is very solid. Thinner cuticle can be grey to greyish-brown, e.g., in

the dorsal opisthosoma of older animals. It was not possible to judge how far this is a true coloration of the cuticle.

The yellow color originates either in the cuticle or in the hypodermis. It was impossible to locate accurately as the yellow color dissolves quickly in 70% alcohol. All that can be seen in the light microscope in individuals with a yellow opisthosoma is a hypodermis poor in dark pigments. The green color, the reddish-brown color of the abdominal stripes as well as the brown and dark brown colors of the opisthosoma-encircling band, the V, the stripes of the pattern and the adult coloration of the females are based in the hypodermis.

The guanine stored in guanocytes provides a white background that causes the colors to be opaque, rather than transparent, and bright

as in the case of the yellow, yellowish-green and green-colored animals. The guanine is not distributed evenly over the opisthosoma. The lateral and dorsolateral guanocytes differ in their guanine content, creating the striped pattern. The opisthosoma's median stripe is caused by the dorsomedian guanocytes, which contain large deposits of guanine, and by the low density of dark pigments in the hypodermis of this area.

Web building behavior.—The spectrum of activities observed in *E. fuliginea* includes walking, construction and destruction of orb-webs, perching in the hub, construction of a hiding place and hiding, catching and eating prey, as well as molting. Although all development stages of *E. fuliginea* show these activities, differences can be found in manner, frequency and timing. Walking constitutes the major part of the moving activities of all age groups. Juvenile spiders were observed walking in short bouts of up to 5 min during the day until day 60, juvenile and adult spiders in bouts from few min to over 1 h during the night.

Juvenile *E. fuliginea* begin orb-web building on day 9 or 10. Up until day 47 they build webs only every second or third day, mostly during the day. Webs of juveniles are small and very variable in form and spatial arrangement, either as horizontal orbs or as orbs which are not plane, thus resembling three-dimensional webs. Older animals shift their web building activities to the night and build bigger, mostly two-dimensional, and more and more asymmetric webs, with the hub being placed near the upper end of the web and the lower capture area being enlarged. Destruction of the webs was observed towards the end of the night. *Eriophora fuliginea* spends 30–70% of its time sitting in the hub of its web. With increasing age, however, fewer individuals are observed sitting on the web during the day: Up to day 60 the yellow and green spiders sit 30–40% of the time in the hub; after day 90 the dark brown spiders spend less than 10% of their time in the hub.

DISCUSSION

Types of color change.—In *E. fuliginea*, the changes in color occur gradually and independently of molting. They are irreversible color changes, not temporary, reversible adaptations to varying backgrounds as can be

the case in species that undergo rapid color changes after disturbances. Examples of reversible color change are *Phonognatha graeffei* (Keyserling 1865) (see Roberts 1936), *Cyrtophora cicatrosa* (Stoliczka 1869) (see Blanke 1975) and *Argiope flavipalpis* (Lucas 1858) (see Edmunds & Edmunds 1986). These species react to disturbances by dropping to the ground and changing from a dark color with a distinctly striped white pattern to a darker, indistinctly patterned color within fractions of a second, thus blending into the background.

This rapid color change is usually based on the contraction of guanocytes (Blanke 1975; Holl 1987) which diminishes the dimension of the white areas. The original color is usually re-established in less than 1 h. Contrary to this rapid and reversible so-called physiological color change (Holl 1987) examples are known of a different reversible color change that takes place slowly and results in different color varieties. This morphological color change (Aechter 1955) is found in animals that adapt their color to their environment once or several times in their lives. One of the best known examples of this slow color change are the crab spiders. The females of *Misumena vatia* (Clerck 1757) can slowly but reversibly adapt their body color to a white or yellow background. Individuals of the araneid *Cyrtophora citricola* (Forsk. 1775) can adapt their color to a new environment over the course of 2–4 wk.

In our study, the juveniles of *E. fuliginea* were observed to be much more frequent in the green color variation in the field than in the laboratory. The varying degrees of the shift from yellow to green at this stage found in the juvenile spiders raised in the laboratory might represent adaptations to the background which are not reversible *per se*, but lose most of their distinctiveness in the final adult color. Experiments with individuals being raised on different backgrounds might provide insights into this phenomenon.

Holl (1987) lists a third type of color change apart from the physiological and the morphological kind, a so-called ontogenetic color change. The resulting coloration is irreversible. According to Holl, it appears to be associated with metamorphosis or molting in arthropods. Since the color change in *E. fuliginea* progresses continuously and indepen-

dently from the molts, it does not conform totally to Holl's definition. Since ontogenetic implies, however, that the color change occurs parallel to the ontogenesis of an animal we feel that the color change of *E. fuliginea* can be classified as such.

Different explanations can be considered for the function or purpose of the various colorations and patterns of *E. fuliginea*. It is rather unlikely that any of the colorations play a role in the thermoregulation of *E. fuliginea* although that function has been reported for *Argiope argentata* (Fabricius 1775) (see Robinson & Robinson 1978). The opisthosoma of *A. argentata*, a spider that is exposed to the sun as it sits in its orb-web during the day, is colored silvery-white in large areas, reflecting the sunlight and thus reducing the thermal effect of this exposure. The yellow forms of *E. fuliginea*, being the lightest color variation of the different forms and therefore possibly playing a similar role as the silvery-white coloration of *A. argentata*, are hardly ever exposed to the sun in their natural habitat. More often, the various colorations and patterns confer a different kind of protection on their bearers. Many species signal to others their dangerousness and/or inedibility by their aposomatic colors.

Function of color change.—*Eriophora fuliginea*, however, belongs to the group of animals that render themselves invisible to their prey as well as to their enemies through their coloration and behavior. The most widely spread strategy for chromatic camouflage is an adaptation to the background. Juvenile *E. fuliginea* sport colors that are found frequently in the vegetation: amber (light orange-brown), yellow, green. A successful camouflage in front of a like-colored background is easily imaginable. Examples are the diverse color variations of the crab spiders with white, yellow, green and even red coloring, depending on their host plant. In Panama, *E. fuliginea* was often observed on the hub of its horizontal orb-web constructed on the upper side of leaves during this "plant-colored" phase. The yellow color of the juvenile spiders might have the additional effect of rendering them invisible to UV-sensitive (and thus red-blind) prey, as is the case in *Misumena vatia* (see Hinton 1976). It is likely that the more contrastingly colored forms of *E. fuliginea* do not expose themselves on leaves, at least not in

the bright daylight. The results of the laboratory observations support this assumption, as a shifting of the activities into the night was observed parallel to this color change. The spotted, mottled and striped patterns of *E. fuliginea* are similar to those of other spiders. Many araneids have developed such outline-dissolving patterns (Robinson & Robinson 1978). This is especially important for species that do not sit directly in front of their backgrounds, as a purely chromatic adaptation would not suffice for camouflage in this case (Robinson & Robinson 1970). According to observations in the field, adult *E. fuliginea* construct their large vertical orb-webs more and more between bushes with advancing age and therefore are further removed from the background than the juvenile spiders that construct their webs between or on leaves. As the potential predators of *E. fuliginea*, like nocturnal lizards, small primates and insectivores, possess much better night vision than humans, this reasoning is still valid in the face of the shift of the activities into the night.

Concluding, the main function of the changing coloration of *E. fuliginea* is likely to be to camouflage the spider adequately during the two different phases of its life. In the juvenile part, spiders are primarily yellow to green, diurnal, and build small symmetric orb webs in large leaves. In the second life part, spiders change to dark brown, are more nocturnal, and build large asymmetric orb webs in vegetation gaps.

ACKNOWLEDGMENTS

We thank the Smithsonian Tropical Research Institute in Panama and the Panamanian authorities (RENARE) for their kind help, Barbara Keller, Gesa Thies and Maria Schiwiek for technical assistance, Sandra Zingg for editing this manuscript and two referees for valuable comments on an earlier version.

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Manuscript received 7 December 1999, revised 6 October 2000.